

## Property fields in a Tortugas Eddy in the southern straits of Florida

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### Abstract

Sea surface temperature imagery, ship-based surveys, and moored current meters described the passage of a Tortugas Eddy as it moved east at ca.  $6 \text{ km day}^{-1}$  through the southern Straits of Florida (SSF). In mid-April 1999 the eddy SST signature extended across half the width of the Straits. While in the western SSF, the eddy center was ca. 30 km seaward of the outer reef. The upper pycnocline, the subsurface chlorophyll *a* maximum (SCM), and nutricline shoaled from ca. 80 m at the eddy edge to  $<60 \text{ m}$  at the center. Maximum chlorophyll *a* concentrations in the SCM were highest near the eddy center, at  $1 \text{ mg m}^{-3}$ , although the depth-integrated concentrations ( $\text{mg m}^{-2}$ ) were similar across the feature. Nutrient-density relationships show nitrate + nitrite, phosphate, and silicate decreased to detection limits at  $\sigma_t < 25.0$ ; the SCM was centered near this isopycnal surface. As the Eddy passed Looe Key ( $81.5^\circ\text{W}$ ) the alongshore currents reversed to the west. During this period high-nutrient, cool waters shoaled near the bottom on the outer reef. By early May, the eddy SST signature was compressed into a thin band of cool surface waters off the Middle to Upper Keys. As the feature moved towards shore in the Middle to Upper Florida Keys, the nitrate + nitrite and chlorophyll concentrations increased in bottom waters along the outer reef. Processes such as internal tidal bores and breaking internal waves are likely responsible for delivering nutrients from Tortugas Eddies to the outer reef in the Middle to Upper Keys.

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### 1. Introduction

Mesoscale eddies influence the vertical distribution and productivity of plankton populations in oligotrophic surface waters. In subtropical gyres, for example, large cyclonic eddies can enhance primary production through the shoaling of the nutricline into the euphotic zone (Falkowski et al.,

1991; McGillicuddy and Robinson, 1997; McGillicuddy et al., 1999). Vortices and eddies with diameters ranging from tens of kilometers to more than one hundred kilometers are characteristic features along the shoreward edge of the Florida Current (Lee and Mayer, 1977; Lee et al., 1995; Shay et al., 1998), although it is not known what effect these features have on the productivity of the Florida Current system. The Florida Current flows through the southern Straits of Florida (SSF) where its surface waters impinge on the outer reefs of the

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Florida Reef Tract. Although the effect of eddies on the productivity of the Florida Current is unknown, it is clear that cyclonic eddies concentrate larvae along the edge of the Florida Current as the features propagate through the Florida Straits (Criales and Lee, 1995). The cross-shore and along-shore flows of eddies enhance the recruitment of larval invertebrates and fish into Florida coastal waters (Lee et al., 1992; Limouzy-Paris, et al., 1997; Porch, 1998; Yeung and Lee, 2002; Sponaugle et al., 2002, 2005). The delivery of larvae from the Florida Current to the outer reefs is further enhanced throughout much of the year by prevailing easterly winds that produce an onshore Ekman transport of surface waters (Lee and Williams, 1999).

The largest eddies in the Florida Current are Tortugas Eddies, cyclonic features with diameters of 100–200 km (Lee et al., 1994). The origin, lifetime, and translation of 11 Tortugas Eddies in the SSF have been described from their sea surface temperature (SST) images by Fratantoni et al. (1998). Cyclonic frontal eddies that propagate along the shoreward edge of the Loop Current can evolve into Tortugas Eddies at the western entrance to the SSF, near the Dry Tortugas (ca. 82°W). Tortugas Eddies are readily identified in SST imagery by their cool surface waters that result from the upwelling of subsurface waters at the eddy center (see Fig. 1). SST imagery shows that Tortugas Eddies often remain stationary near the Dry Tortugas for weeks to months, and subsequently propagate east following the approach of a second frontal feature (Fratantoni et al., 1998). Warm streamers are frequently entrained along the leading edge of the Eddy and wrap around, and into, the cold core (Fig. 1c–e). The SST signatures of Tortugas Eddies can persist for 50–140 days. As the features move east their cross-stream diameter decreases as their length and speed increase. The surface temperature signature of an Eddy is typically erased to the east of 80°W where the Straits of Florida turns to the northeast and its width decreases.

Although SST imagery has described the formation and history of the surface signature of Tortugas Eddies, there are few observations of their subsurface structure in relation to the surrounding Florida Current. The hydrographic structure, nitrate and chlorophyll *a* distributions have been mapped along the shoreward edge of two Tortugas Eddies near the Dry Tortugas, at the western end of the SSF (Lee et al., 1994), and a third eddy further east near the Middle Keys (Lee et al., 1992). The three regions of

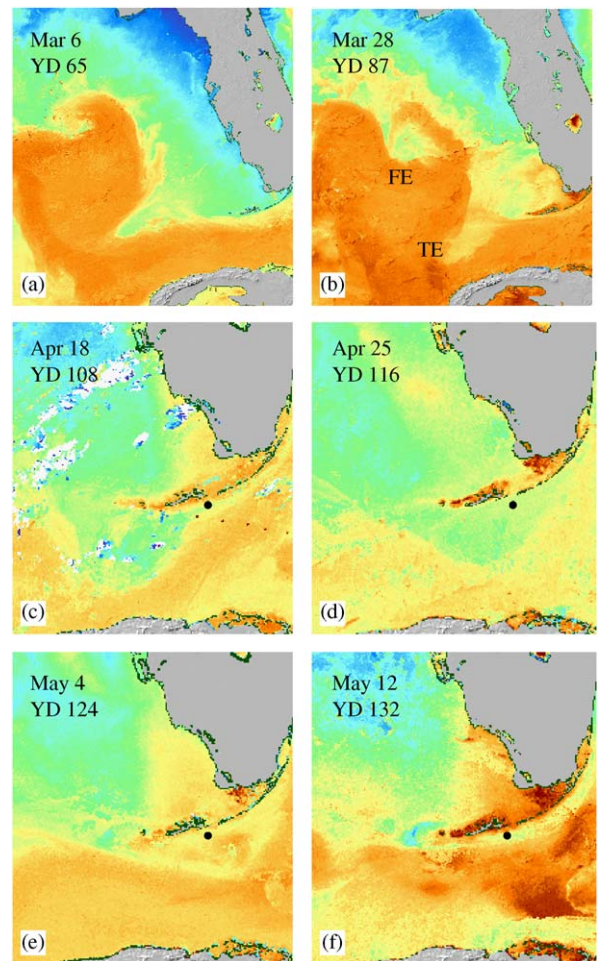


Fig. 1. Sea surface temperature (SST) images of the Tortugas Eddy in the Gulf of Mexico and southern Straits of Florida between March and May 1999. Three-day composite AVHRR SST images, provided courtesy of the John Hopkins University, are presented for March 6 (a) and 28 (b), April 18 (c) and 25 (d), May 4 (e) and 12 (f). Position of the Tortugas Eddy (TE) and a Frontal Eddy (FE) are indicated in 1b. The solid symbol (●) is the location of Looe Key.

the Florida Keys include the Lower Keys, the Middle Keys, and the Upper Keys (see Fig. 2a). Most studies of nutrient and chlorophyll *a* distributions in the oligotrophic Florida Current have concentrated on the nearshore waters of the Florida Reef Tract (e.g., Szmant and Forrester, 1996; Keller and Itkin, 2002). At the outer reef, at the 30–40 m isobaths, surface waters are oligotrophic with dissolved inorganic nitrogen and phosphorus concentrations  $<0.1 \text{ mmol m}^{-3}$ , and chlorophyll *a* concentrations  $<0.1 \text{ mg m}^{-3}$ . To our knowledge, however, there are no observations of pigment and nutrient distributions across the width of a Tortugas Eddy.

Transects in the SSF cannot be completed without entering Cuban waters, so recent studies of nutrient and plankton distributions that extend across the Florida Current are north of the SSF, between Miami and the Bahamas (e.g., Vargo, 1968). A series of cruises between 1960 and 1964 established that the surface waters of the Florida Current east of Miami are oligotrophic with dissolved inorganic phosphate  $<0.1 \text{ mmol m}^{-3}$  (Corcoran and Alexander, 1963). Euphotic zone depths are approximately 100 m in the eastern

Florida Current, and a subsurface chlorophyll maximum (SCM) of  $0.20\text{--}0.50 \text{ mg chlorophyll } a \text{ m}^{-3}$  is located in the upper pycnocline (Alexander et al., 1961). Surface chlorophyll concentrations derived from ocean color sensors verify the earlier ship-based observations. Surface chlorophyll  $a$  concentrations in the Florida Current from SeaWiFS imagery vary from  $0.05$  to  $0.09 \text{ mg chlorophyll } a \text{ m}^{-3}$  (González et al., 2000). These values are comparable to the oligotrophic Gulf of Mexico and Caribbean Sea. In summer the surface chlorophyll  $a$  concentrations throughout the Yucatan Channel, Loop Current, and Straits of Florida average  $0.06 \text{ mg m}^{-3}$ . An annual maximum occurs between October and March when surface chlorophyll  $a$  levels can reach  $0.15 \text{ mg m}^{-3}$ .

In May 1999 we surveyed density, nutrient and chlorophyll distributions in a Tortugas Eddy as it passed through the SSF. Our main objective was to determine if the nutricline shoaled at eddy center, and if it did, was phytoplankton pigment biomass enhanced relative to that in the contiguous Florida Current. Elevated phytoplankton biomass in Tortugas Eddies could enhance primary productivity within the feature, and thereby contribute to sustaining fish and invertebrate larvae. In addition to the shipboard observations, three instrument moorings recorded the passage of the Tortugas Eddy at Looe Key (LK), a reef south of Big Pine Key that has been designated a National Marine Sanctuary (Causey, 2002). Currents and surface temperatures have been continuously monitored at LK since 1989. Consequently, the short-term and seasonal variability in currents and temperature are well documented at this reef as summarized by Lee and Williams (1999).

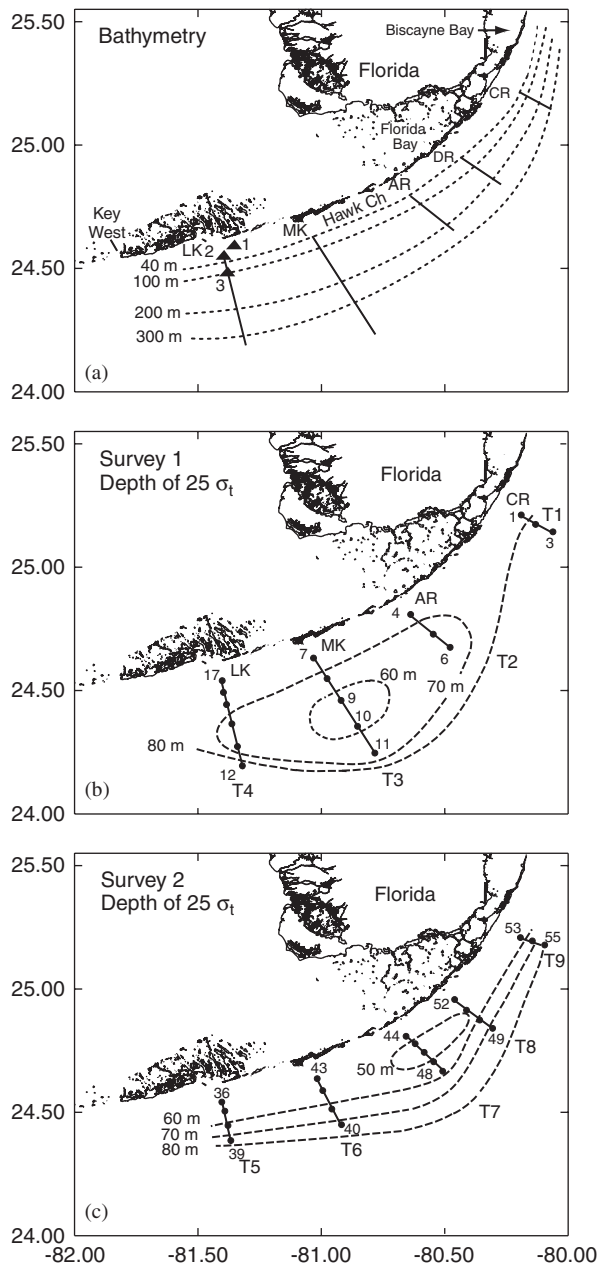


Fig. 2. (a) Bathymetry of the study region with the outer reef designated by the 40 m isobath. The offshore extension of the 200 and 300 m isobath reflect the Pourtales Terrace. The five lines correspond to transects in Surveys 1 and 2, as in b. and c. The Transects extend seaward from Carysfort Reef (CR), Davis Reef (DR), Alligator Reef (AR), Marathon Key (MK), and Looe Key Reef (LK). The three triangles near Looe Key correspond to mooring 1 (Hawk Channel, 9 m), mooring 2 (Looe Key, 25 m), and mooring 3 (ADCP at 100 m isobath). (b) Subsurface structure of the Tortugas Eddy as defined by the depth of the  $25.0\sigma_t$  surface in Survey 1. The four transects in Survey 1 correspond to T1–T4, extending seaward from CR, AR, MK, and LK, respectively. (c) Subsurface structure of the Tortugas Eddy as defined by the depth of the  $25.0\sigma_t$  surface in Survey 2. The five transects in Survey 2 correspond to T5–T9, extending seaward from LK, MK, AR, DR, and CR, respectively. Inshore of the reefs the water column was uniformly mixed at  $\sigma_t < 25.0$ .

## 2. Methods

### 2.1. SST imagery

The passage of the Tortugas Eddy through the SSF is described from SST imagery acquired by the Advanced Very High Resolution Radiometer (AVHRR). Three-day composite images from April to May 1999 were obtained from the Ocean Remote Sensing group of the Applied Physics Laboratory at the Johns Hopkins University. The SST chronology of the feature is at <http://fermi.jhuapl.edu/avhrr/index.html>. The complete imagery shows that a frontal eddy formed on the western side of the Loop Current downstream of Campeche Bank in early December 1998. The feature moved to the western entrance of the SSF during the next three months (Fig. 1a), and by March it had evolved into a Tortugas Eddy at the western end of the SSF (Fig. 1b).

### 2.2. Surveys

The eddy structure was mapped in two surveys with the University of Miami's R.V. *Calanus*. The surveys were composed of four or five transects, and each transect had three to six conductivity-temperature-depth (CTD) stations. Survey 1 (S1) was completed between May 5 and 7 with four transects designated as T1–T4 (Fig. 2b). The transects were run east-to-west, extending seaward from the outer reef at Carysfort Reef (CR), Alligator Reef (AR), Marathon Key (MK) and LK. At each of the CTD stations a Seabird Model 9 CTD was lowered to within 5 m of the bottom, or to a maximum depth of 200 m. The rosette had twelve 10 l Niskin bottles with external closing mechanisms. Survey 1 required 48 h to complete, so the property distributions are not truly synoptic since the Eddy was moving east at ca.  $6 \text{ km day}^{-1}$  as the ship steamed west. One week later, on May 12, the SST signature of the Eddy was greatly reduced (Fig. 1f). Survey 2 (S2) was completed between May 12 and 14 when the feature was centered offshore of AR and Davis Reef (DR) (Fig. 2c). Five transects were completed during the second survey with nineteen CTD stations (CTD 36 to CTD 55). The five transects, designated T5–T9, were run west-to-east from LK, MK, AR, DR, and CR (Fig. 2c).

Temperature, conductivity and chlorophyll *a* fluorescence were recorded on each CTD downcast to select sampling depths for the upcast. Three to

seven depths were sampled between the surface and the bottom of the cast based on the vertical structure of the density and chlorophyll *a* profiles. The base of the surface mixed layer was defined as the depth where the change in the vertical density profile exceeded the surface value by  $0.125 \text{ kg m}^{-3}$  (e.g., Babu et al., 2004). For chlorophyll analyses we filtered duplicate 200 ml aliquots from each Niskin bottle onto Whatman GF/F filters at  $<100 \text{ mmHg}$  vacuum. The filters were stored at  $-20^\circ\text{C}$  and pigment analyses were completed within 3 weeks of the cruise. Pigments were extracted with methanol as described by Holm-Hansen and Riemann (1978) with fluorescence read before and after acidification on a Turner Designs TD-700 fluorometer calibrated with chlorophyll *a* standards from Sigma Chemical Corp. A linear relationship existed between the in situ fluorescence recorded by the CTD Wetstar fluorometer (volts) and the total chlorophyll *a* concentrations derived from total chlorophyll *a*, as the sum of extracted chlorophyll plus phaeopigments. A total of 117 samples yield the relationship Wetstar fluorometer voltage (volts) =  $(1.53 \times \text{total chlorophyll } a) + 0.03$  (Fig. 3). The transformed relationship, total chlorophyll *a* ( $\text{mg m}^{-3}$ ) =  $0.722 \text{ (volts)} + 0.134$ , was used to estimate in situ chlorophyll concentrations from the Wetstar fluorometer profiles. In situ chlorophyll concentrations extrapolated from the Wetstar fluorometer are designated as

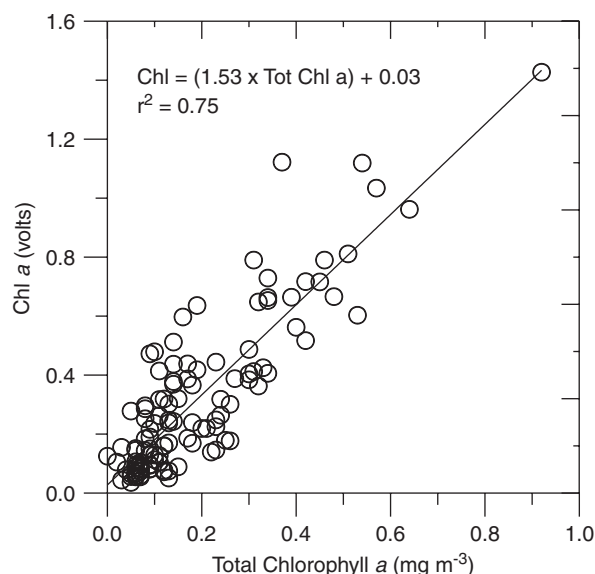


Fig. 3. Chlorophyll *a* fluorescence (Chl *a*) from the Seapoint CTD fluorometer as a function of total chlorophyll *a* ( $\text{mg m}^{-3}$ ) extracted from discrete samples. Total chlorophyll is equal to the sum of chlorophyll *a* and phaeopigments.



Chl *a* ( $\text{mg m}^{-3}$ ). The depth-integrated standing stock of total chloropigment *a* ( $\Sigma$ ) as  $\text{mg m}^{-2}$ , was calculated by the trapezoidal summation of Chl *a* at 1 m intervals between the surface and a maximum depth of 150 m, or the bottom of the profile where the bottom depth was  $<150$  m.

Nutrient samples were filtered through Whatman 0.45  $\mu\text{m}$  pore cellulose nitrate filters and frozen in acid-cleaned polypropylene test tubes. Analyses for dissolved inorganic nitrate and nitrite, phosphate, and silicate were conducted with an automated analyzer as described by Gordon et al. (1993). No ammonium analyses were attempted since the samples had to be stored frozen before the analyses could be completed ashore.

### 2.3. Moored instrumentation

Three moorings were located near LK Reef (Fig. 2a). The moorings were deployed from early April to late September, 1999. Mooring 1 was deployed on April 6, 1999 at the 8 m isobath in Hawk Channel ( $24^{\circ}35.33'\text{N}$ ,  $81^{\circ}23.158'\text{W}$ ), approximately 2 km northwest of LK Reef. Hawk Channel parallels the Keys inshore of the Florida Reef Tract (see Fig. 2a). Mooring 1 had a MicroCat at 2 m, two TSKA temperature loggers at 4 and 6 m, respectively, and an Aanderaa current meter at 6 m. Mooring 2 was located approximately 1 km seaward of LK Reef in 25 m of water ( $24^{\circ}32.55'\text{N}$ ,  $81^{\circ}24.13'\text{W}$ ). It contained a Sontek current meter at 5 m, two TSKA temperature sensors at 10 and 15 m, respectively, and an Aanderaa current meter at 21 m. A SeaBird Microcat (temperature and conductivity), pulsed oxygen probe, and Wetstar fluorometer were deployed at 9 m depth on the mooring line on April 28. Seawater was pumped through the Microcat and Wetstar fluorometer at 10 min intervals from a Seabird pump controlled by a Tattletale Model 8 microcontroller which also regulated the power supplies and recorded data. Fouling of the fluorometer and Microcat was minimized by a bromine canister on the water intake (Davis et al., 1997). Mooring 3 was deployed at the 100 m isobath seaward of LK Reef at  $24^{\circ}30.159'\text{N}$ ,  $81^{\circ}23.825'\text{W}$ . This mooring was instrumented with a Microcat at 6 m and a bottom-mounted 300 kHz ADCP at 100 m. Six TSKA temperature sensors were located on mooring 3 at 15, 25, 35, 50, 70 and 95 m.

## 3. Results

### 3.1. Timeline of Eddy evolution

During March and early April 1999 the Tortugas Eddy was located southwest of the Dry Tortugas (Fig. 1b). By April 18 the feature had entered the western SSF (Fig. 1c). The Eddy moved into the SSF following the approach of a second frontal eddy as seen in Fig. 1b; this sequence often initiates the eastward motion of a Tortugas Eddy into the SSF (Fratantoni et al., 1998). In the last week of April the Eddy surface signature extended across half the width of the SSF with the coolest surface waters centered near  $81.5^{\circ}\text{W}$  (April 25, Fig. 1d). One week later, on May 4, the Eddy center was southeast of LK Reef at  $81^{\circ}\text{W}$  (Fig. 1e). The eastward motion of the Eddy between April 25 and May 4 corresponds to an average easterly speed of  $6 \text{ km day}^{-1}$ , similar to the speeds of Tortugas Eddies reported by Fratantoni et al. (1998).

The Tortugas Eddy approached LK in late April with the Eddy center passing the moorings between April 25 and May 4 (Fig. 1d and e). At the beginning of the second survey, on May 12, the surface signature of the Eddy had been reduced to a thin band of cool surface water adjacent to the outer reef from the Lower Keys north to Biscayne Bay (Fig. 1e).

### 3.2. Surveys

The subsurface structure of the Tortugas Eddy is defined here by the depth of the  $25\sigma_t$  isopycnal surface. This density surface coincided approximately with the upper pycnocline, the nutricline, and the SCM. In Survey 1 the  $25\sigma_t$  surface shoaled from 80 m at CTD 11, near the seaward edge of the feature, to  $<60$  m at the eddy center between CTD 9 and 10 (Fig. 2b). The shoaling of the pycnocline corresponds to the area of cool surface waters in the SST imagery of the Eddy (Fig. 1e). The shoaling of the pycnocline located the Eddy center ca. 30 km from the outer reef in 200 m of water. At the CTD stations near the Eddy center the surface temperatures were  $26.1\text{--}26.2^{\circ}\text{C}$ , as compared to  $28^{\circ}\text{C}$  in the adjacent Florida Current. The  $\sigma_t$  and SST distributions also show that the Eddy surface front extended  $>130$  km along the coast and 70 km offshore, or half the width of the SSF (Fig. 1d and e).

During Survey 1 the temperature and chlorophyll profiles on the outer reef indicate that the water column was well mixed. There was little vertical structure evident in either temperature or chlorophyll *a* profiles at MK and LK, although slightly elevated pigment concentrations were found within 5–15 m of the bottom at CR and AR (Fig. 4). Shoreward of the Eddy center, at MK and LK, the water column was well-mixed with chlorophyll *a* concentrations  $<0.2 \text{ mg m}^{-3}$ . A limited number of nitrate measurements on the outer reef indicate that concentrations were  $<0.4 \text{ mmol NO}_3 \text{ m}^{-3}$ . Chlor-

ophyll and nutrient concentrations on the Florida Keys outer reef are typically  $0.2\text{--}0.5 \text{ mg Chl } a \text{ m}^{-3}$ , with maximum nitrate concentrations on the order of  $0.5 \text{ mmol m}^{-3}$  (Szmant and Forrester, 1996).

Transect 1 extended offshore of CR in the Upper Keys, upstream of any surface signature of the Eddy. As shown above, there was little vertical stratification on the outer reef at CR (Fig. 4). However, density and chlorophyll *a* profiles at CTD 2, located 6 km offshore of Carysfort on the 160 m isobath, reveal a mixed layer  $<15 \text{ m}$  deep and peak

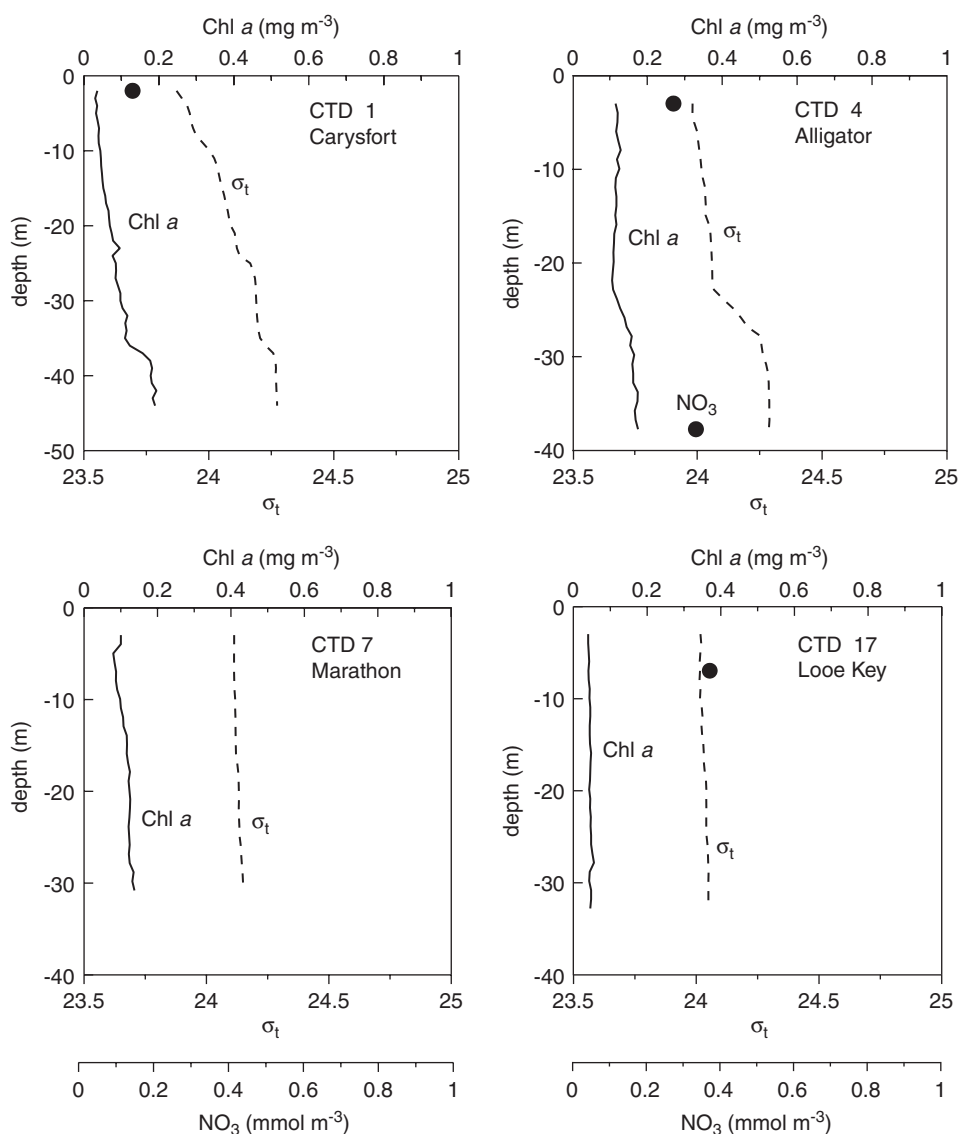


Fig. 4. Vertical profiles of density (dashed line) and chlorophyll (solid line), and nitrate (●) concentrations at the outer reef stations in the four transects of Survey 1. Vertical profiles of Chl *a* are extrapolated from the Seapoint fluorometer voltage as in Fig. 3.

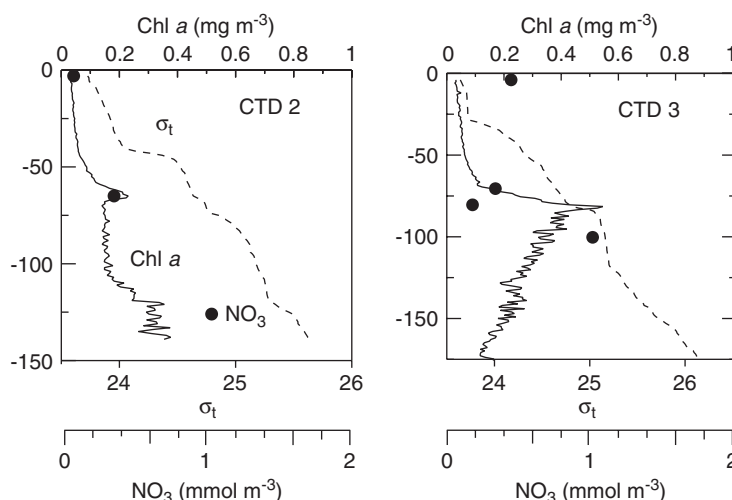


Fig. 5. Vertical profiles of density (dashed line) and Chl *a* (solid line) and nitrate (●) at CTD stations 2 and 3 in Transect 1 (symbols as in Fig. 4). These two stations were seaward of the outer reef and downstream of the eddy. The profiles illustrate the vertical structure of the Florida Current in the absence of the eddy.

SCM chloropigment *a* concentrations of  $0.4 \text{ mg m}^{-3}$  (Fig. 5). At CTD 3, 9 km further offshore, the surface mixed layer extended to almost 20 m with SCM pigment concentrations of  $1 \text{ mg m}^{-3}$  in the upper pycnocline at 75 m.

Transects 2 through 4 were completed on May 6 and 7, with T3 crossing the eddy center. This 50 km-long transect extended from the outer reef at MK (CTD 7, 44 m bottom depth) to CTD 11 where the water depth exceeded 300 m. The pycnocline, SCM, and nutricline shoaled at the Eddy center between stations CTD 9 and 10 (Figs. 2 and 6). Maximum Chl *a* concentrations in the SCM increased from  $0.6 \text{ mg m}^{-3}$  at the inshore edge of the Eddy (CTD 8) to  $0.9 \text{ mg m}^{-3}$  at CTD 9 and 10. The SCM was defined by a sharp peak at the Eddy center, while further offshore at CTD 11, the vertical distribution had a relatively broad maximum with peak Chl *a* concentrations  $< 0.6 \text{ mg m}^{-3}$ . The broad peak in the Chl *a* profile at CTD 11 is typical of many Gulf Stream profiles (e.g., Ortner et al., 1980; Hitchcock et al., 1993) and was similar to that seen at CTD 3.

In general, the SCM coincided with the upper pycnocline across the width of the Eddy. This pattern is typical in the subtropical North Atlantic where light intensity approaches compensation intensities in the upper pycnocline (e.g., Ortner et al., 1980; McGillicuddy et al., 1999; Siegel et al., 1999). Maximum Chl *a* concentrations in the Tortugas Eddy profiles also coincided with maximum stability in the upper pycnocline, as defined

by the Brunt-Väisälä frequency (Fig. 6, lower panels). This vertical pattern occurs throughout the North Atlantic's subtropical waters (Agustí and Duarte, 1999). However, vertical stability was not invariably an indicator of elevated chlorophyll fluorescence. For example, at CTD 8, 10 and 11, several 'peaks' occurred in the BV frequency profile within the upper 50 m with no increase in Chl *a*.

Depth-integrated pigment concentrations were estimated from the Chl *a* profiles to determine if chloropigment was elevated at the Eddy center. At the 12 CTD stations seaward of the outer reef the depth-integrated Chl *a* concentrations ranged from a minimum of  $18.8 \text{ mg m}^{-2}$  to a maximum of  $31.9 \text{ mg m}^{-2}$  at CTD 5 and 11, respectively. The average depth-integrated pigment concentration was  $24.3 \pm 4.2 \text{ mg m}^{-2}$  ( $n = 12$ ) at these stations, as compared to 26.1 and  $26.31 \text{ mg m}^{-2}$  at CTD 9 and 10, respectively. Thus the increase in chloropigments in the SCM at the Eddy center did appear to not enhance the depth-integrated pigment concentration.

The second survey was completed after the surface signature of the Eddy had collapsed into a narrow band of cool surface water (Fig. 1f). The width of the Eddy, as defined by the  $25.0\sigma_t$  surface, decreased as the feature moved east (Fig. 2c). In Survey 1 the Eddy center was 30 km from the outer reef at bottom depths  $> 200 \text{ m}$ ; in Survey 2, in contrast, the Eddy center was  $< 20 \text{ km}$  from the outer reef and at bottom depths of 150 m.

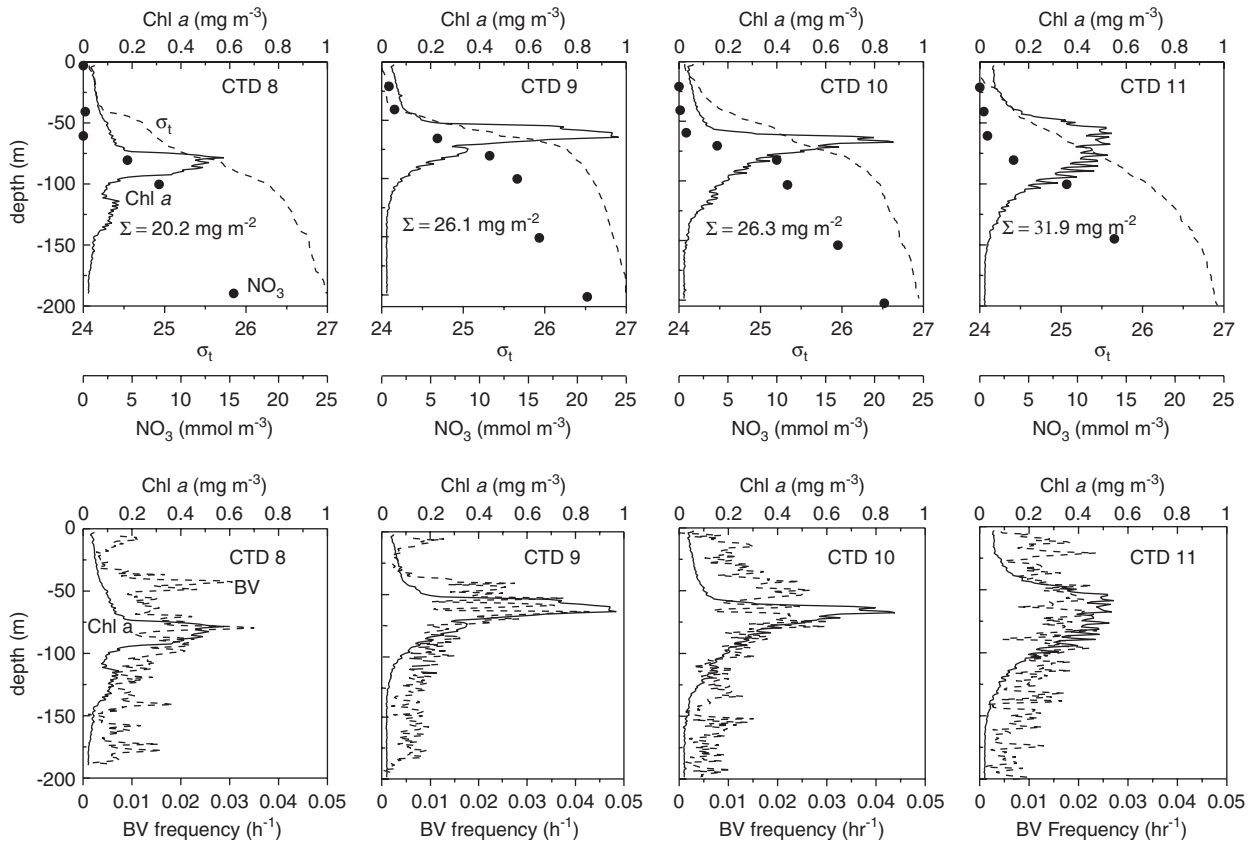


Fig. 6. Top: Vertical profiles of density (dashed line) and chlorophyll *a* fluorescence (solid line) and nitrate concentrations from discrete samples (●) at CTD stations 8–11. These stations crossed the eddy center in Transect 3 on May 5. The eddy center, as defined by the shoaling of the pycnocline, was near CTD stations 9 and 10. The depth-integrated chlorophyll *a* concentration ( $\Sigma$ ,  $\text{mg m}^{-2}$ ) is summed from the Chl *a* concentrations at 1 m intervals between the surface and 150 m. Bottom: Profiles of chlorophyll *a* fluorescence (solid line) and the Brunt-Väisälä frequency (dashed line) at CTD stations 8–11.

The shoaling and shoreward movement of the Eddy influenced property distributions along the outer reef tract in the Middle to Upper Keys. In general, the chlorophyll and nitrate concentrations on the outer reef were higher in Survey 2 than in Survey 1. Chlorophyll concentrations near the bottom at MK and CRs, for example, ranged from 0.4 to 0.8  $\text{mg Chl } a \text{ m}^{-3}$  in Survey 2, or 2–4-fold higher than in Survey 1, (cf. Figs. 4 and 7). Nitrate concentrations near the bottom on the outer reef also increased in early May, attaining peak concentrations of 0.2–0.4  $\text{mmol NO}_3 \text{ m}^{-3}$  at MK, AR, and CR (Fig. 7). At DR, in contrast, the pigment and nitrate values were similar to those observed in Survey 1 at nearby Carysfort and ARs (cf. Figs. 4 and 7). Thus the shoreward movement of the eddy did not uniformly enhance the near-bottom pigment and nitrate concentrations along the entire outer Reef Tract. This indicates that

physical processes below the mesoscale are likely important in the delivery of pigment and nutrients to the outer reef.

Transect 7 crossed the Eddy center on May 13, one week after it was surveyed in T3. On May 13 the center of the Eddy was between CTD 46 and 47, in approximately 150 m of water (Fig. 8). At the Eddy center the 25.0  $\sigma_t$  isopycnal surface was at ca. 50 m where peak Chl *a* concentrations ranged from 0.6 to 0.8  $\text{mg m}^{-3}$  (Fig. 8). Depth-integrated chlorophyll concentrations were similar to those found in Survey 1. The mean depth-integrated Chl *a* concentration for the 15 stations seaward of the 100 m isobath in Survey 2 was  $21.9 \pm 3.4 \text{ mg m}^{-2}$ . As in Survey 1, high chlorophyll *a* concentrations often coincided with high B–V frequencies near the upper pycnocline (Fig. 8, lower panel), although in the surface layer there was no direct correspondence between the profiles of BV frequency and Chl *a*.



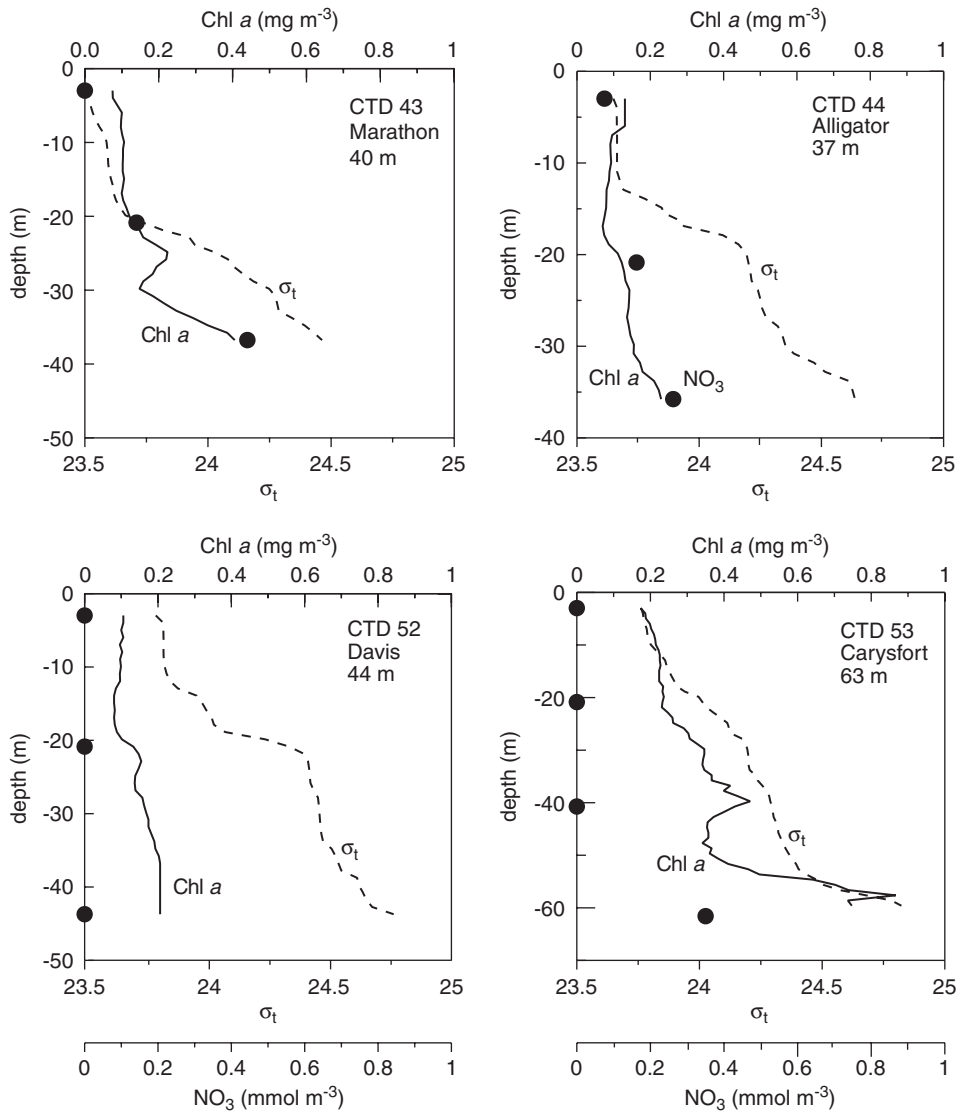


Fig. 7. Vertical profiles of density (dashed line) and chlorophyll *a* fluorescence (solid line), and nitrate concentrations (●) at four stations located at the outer reef tract during Survey 2. These four CTD stations are from Transects T6–T9.

### 3.3. Nutrient–density relationships

Surface waters in the Tortugas Eddy were oligotrophic with inorganic nutrient concentrations at, or near, the detection limit of the autoanalyzer methods. The nitrate + nitrite, phosphate and silicate concentrations were typically  $<0.5 \text{ mmol m}^{-3}$  on the isopycnal surfaces  $<25\sigma_t$  (Fig. 9). These density surfaces were shallower than 60 m in Survey 1, and in Survey 2 shallower than 50 m. Mixed layer depths were  $<15 \text{ m}$  across the width of Eddy in both surveys. Chl *a* also exhibited a fairly consistent

relationship with the vertical density structure at the Eddy center. Peak Chl *a* concentrations were centered in the pycnocline between the  $25.0\text{--}25.5\sigma_t$  surfaces (Fig. 9d). Enhanced chlorophyll concentrations in the pycnocline likely correspond to a depth interval with considerable biogenic nutrient uptake, given low nutrient concentrations in the overlying surface waters.

Nutrient–density relationships were similar in Surveys 1 and 2 at depths corresponding to density surfaces  $>27.0\sigma_t$ . These density surfaces were generally at 150–200 m. Mean N:P ratios at  $\sigma_t =$

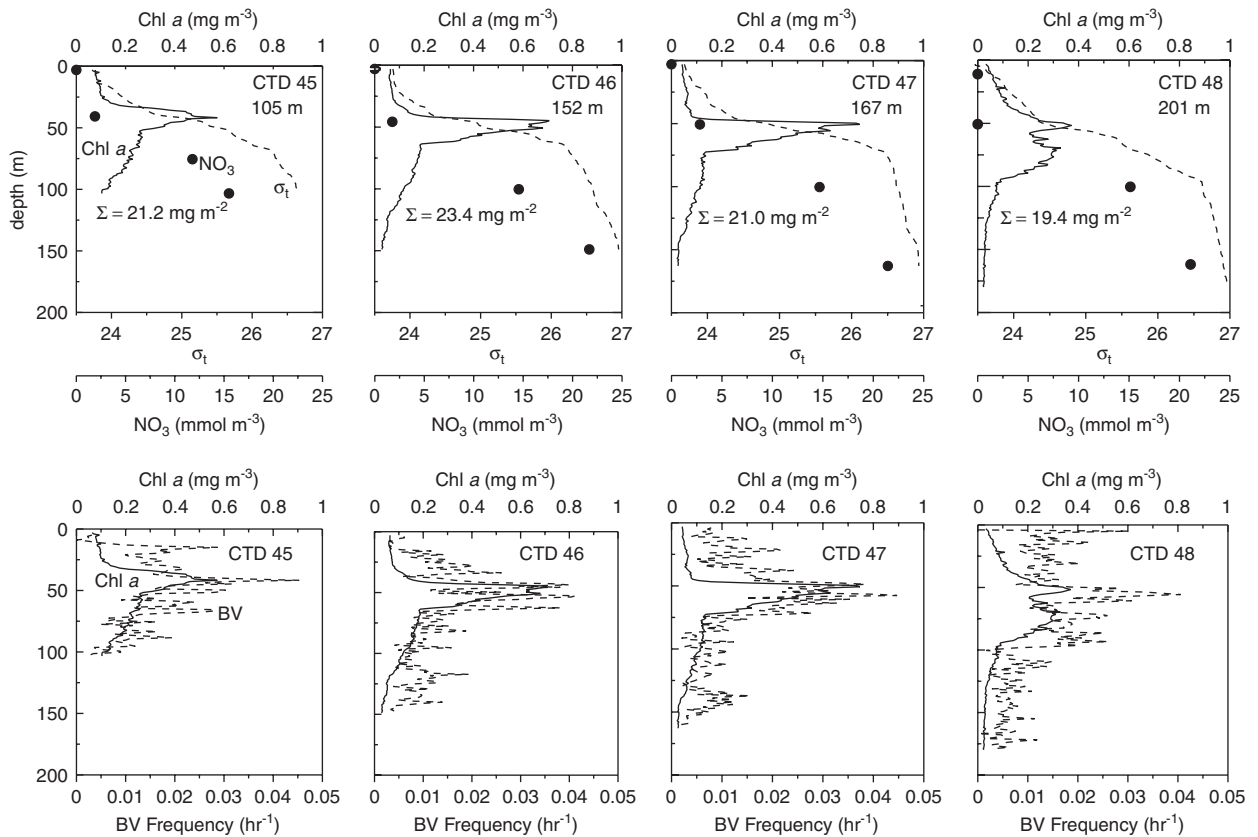


Fig. 8. Top: Vertical profiles of density (dashed line), chlorophyll *a* fluorescence (solid line), and nitrate concentrations (●) from CTD stations 45–48 in Transect 7 which crossed the eddy center on May 13. The depth-integrated chlorophyll *a* concentration ( $\Sigma$ ,  $\text{mg m}^{-2}$ ) is summed from the surface to 150 m, or to the bottom at shallower stations. Bottom: vertical profiles of chlorophyll *a* fluorescence (solid line) and the Brunt Väisälä frequency (dashed line) at CTD stations 45–48. The eddy center was near CTD stations 45 and 46.

26.9–27.10 were  $19.86 \pm 2.5$  (Survey 1) and  $15.0 \pm 3.7$  (Survey 2). Although the ratio was slightly higher in Survey 1, there was no statistically significant difference in the N:P ratios between the two surveys. Ratios of N:Si were  $2.11 \pm 2.5$  (Survey 1) and  $2.28 \pm 2.5$  (Survey 2), also statistically equivalent in both surveys ( $p = 0.05$ ). At shallower depths, however, there was considerable scatter in the nitrate + nitrite, phosphate, and silicate values within the upper pycnocline, at  $24.0\text{--}25.0\sigma_t$ , in Survey 2 (Fig. 9a–c). The increased nutrient concentrations in the upper pycnocline may reflect enhanced mixing near the outer reef by processes such as tidal bores and internal waves, as documented by Leichter et al. (1996, 1998). A shoaling of the SCM was also evident in the upper pycnocline in Survey 2, with peak chlorophyll concentrations centered at the  $24.5\sigma_t$  surface, as compared to the  $25.0\text{--}25.5\sigma_t$  isopycnal surfaces in Survey 1 (Fig. 9d).

### 3.4. LK Reef time series

Time series of currents and temperature at LK document the movement of the Tortugas Eddy along the outer reef tract in April and May. Subtidal time series of alongshore currents show the eddy had a strong influence on the current field between the 100 m isobath and the nearshore waters of Hawk Channel over the 6-week interval between April 12 and May 28 (Fig. 10). As the Eddy approached the LK moorings in mid-April, there was a rapid decrease in velocity coupled with a reversal in flow at all three moorings (Fig. 10). The westward flow at Hawk Channel to the 100 m isobath continued as the cyclonic Eddy passed the moorings between mid-April and late May. Downstream flows subsequently increased to  $> 100 \text{ cm s}^{-1}$  on May 28 as the trailing edge of the Eddy passed LK Reef. This sequence occurred as the Eddy

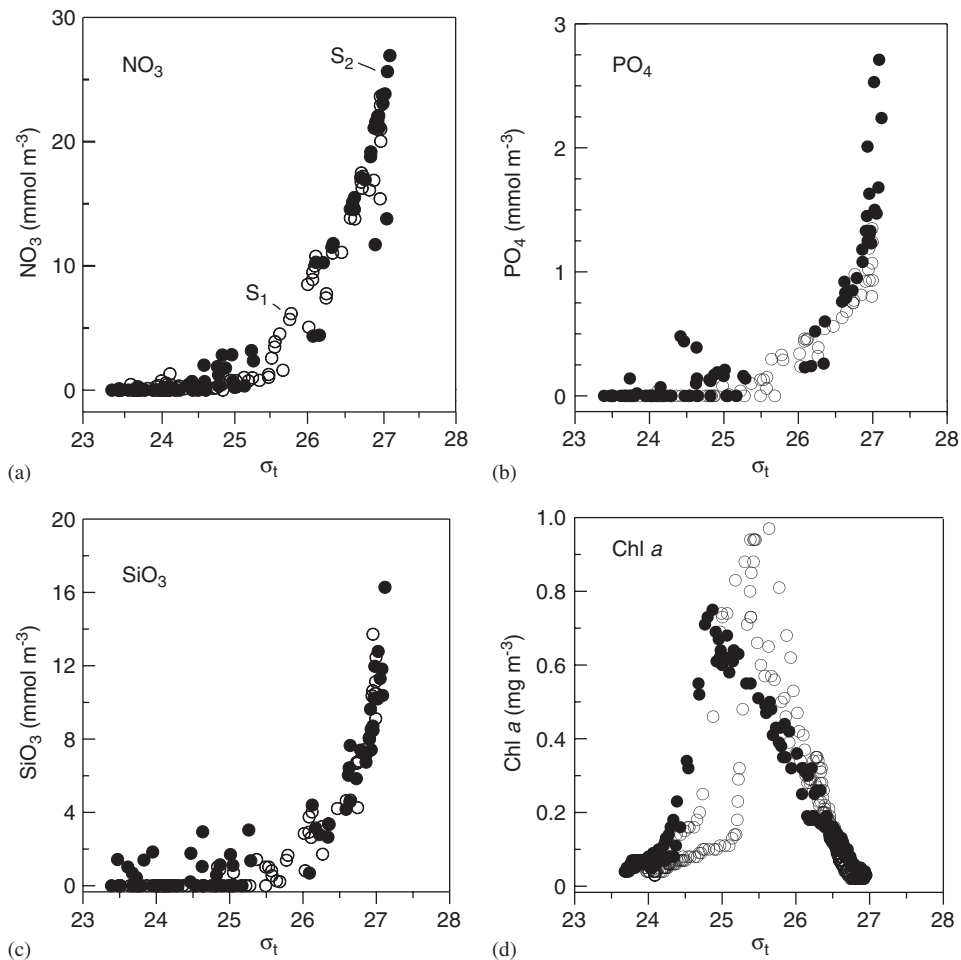


Fig. 9. Concentrations of (a) nitrate, (b) phosphate, and (c) silicate as a function of density at CTD stations from Survey 1 ( $\circ$ ) and Survey 2 ( $\bullet$ ). (d) Chlorophyll *a* concentrations, extrapolated from chlorophyll fluorescence (Chl *a*), as a function of density at CTD stations near the eddy center in Survey 1 (CTD 9 and CTD 10) and Survey 2 (CTD 45 and CTD 46).

elongated and the Florida Current surface front moved toward shore in the Middle to Upper Keys (Fig. 1f). A series of smaller, sub-mesoscale vortices generated brief periods of counter-currents between April 17 and 29, and again from May 2 to 8. These events are designated in Fig. 10 as sub-mesoscale eddy 1 and 2.

Subtidal temperature time series also illustrate the passage of the Eddy. Temperature increased at 70 and 95 m as the feature approached the 100 m mooring near LK (April 9–16 in Fig. 11). This increased temperature indicates that warm waters of the Eddy extended to the bottom on the outer reef. The increase in subsurface temperatures coincided with the offshore movement of the Florida Current front as the Eddy center approached LK. A second temperature increase occurred as the currents

reversed during the passage of sub-mesoscale eddy 2 between May 2 and 6. As the Tortugas Eddy exited LK, the Florida Current front converged towards shore, and temperatures at depths below 70 m decreased by 7–10 °C (Fig. 11).

When dissolved inorganic nitrogen concentrations are regressed against their corresponding temperatures from the CTD casts, a strong inverse linear relationship is evident at temperatures < 22.0 °C (Fig. 12). This relationship is described by

$$\text{NO}_3 = 46.322 - (2.043 \times T) \quad [r^2 = 0.96], \quad (1)$$

where *T* is temperature (°C). The strong relationship permits an estimate of in situ nitrate concentrations, as previously computed in the Gulf Stream front off the southeast continental US by Lee et al. (1991). Subtidal nitrate time-series derived from the TSKA

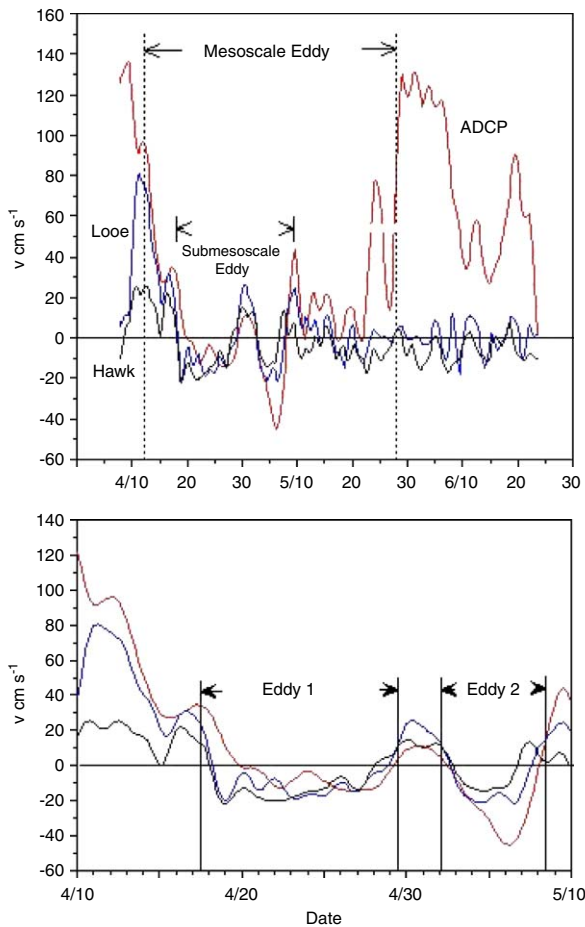


Fig. 10. Top: Subtidal time series of alongshore currents between April and May 1999 at the three moorings located near Looe Key. Currents are from 4 m depth on the Hawk Channel mooring (mooring 1 at 8 m isobath), 7 m depth on the Looe Key reef mooring (mooring 2 at 25 m isobath) and 30 m depth on the outer reef ADCP mooring (mooring 3 at 100 m isobath). Sub-mesoscale eddies passed by the moorings between April 17 and 29, and May 2 and 9. Bottom: An expanded view of the alongshore currents during the passage of the two sub-mesoscale eddies between April 17 and 29 (eddy 1) and May 2–9 (eddy 2).

temperature records on the 100 m mooring and the temperature-nitrate relationship are presented in Fig. 13. In April large decreases occurred in nitrate concentrations at depths  $>70$  m as the Tortugas Eddy moved towards LK. During this period the deeper, cooler waters of the Florida Current moved offshore as the warmer surface waters of the Tortugas Eddy flowed onto the outer reef. As the Eddy exited LK there was a rapid increase of ca.  $5\text{--}24\text{ mmol NO}_3\text{ m}^{-3}$  at depths of 70 and 95 m. This increase in nitrate concentrations corresponds to the

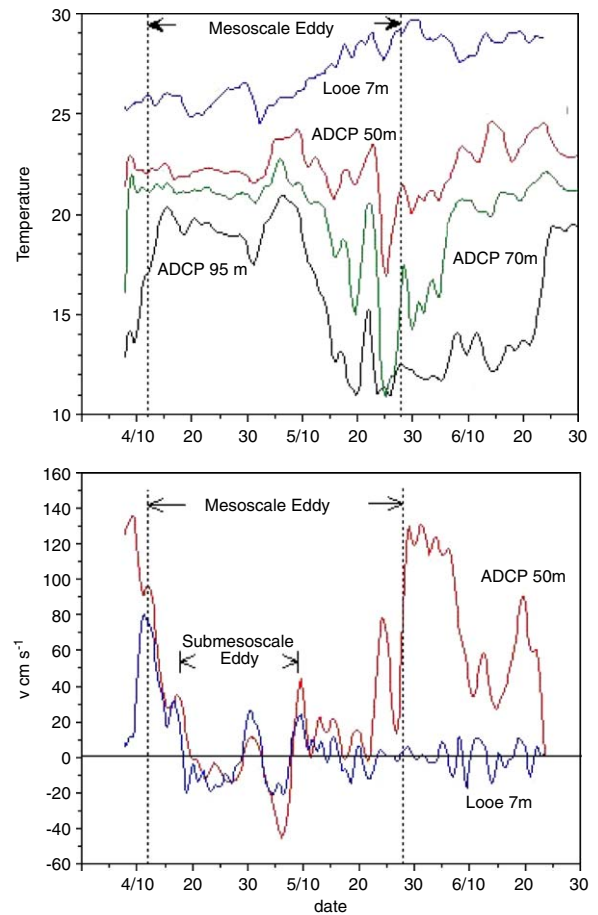


Fig. 11. Top: Temperature time series at depths of 50, 70 and 95 m on the ADCP mooring located at the 100 isobath. The temperature record from a thermistor at 7 m depth on the Looe Key mooring (25 m isobath) is included for comparison. The temperature records show that the eddy passage influenced temperature across the shelf, with the strongest effect at the 100 m isobath. Bottom: The alongshore currents from 7 m at the Looe Key mooring (25 m isobath) and at 30 m from the ADCP mooring (100 m isobath). The duration of the Tortugas eddy is designated as Mesoscale Eddy. The bottom panel includes the interval during the passage of the sub-mesoscale eddies between April 17 and May 9.

arrival of cooler subsurface waters as the Florida Current moved towards shore.

Short-term variability was also evident in temperature records from LK Reef on time scales less than one day (data not shown). Temperature changes of  $1\text{--}2^\circ\text{C}$  occurred over several hours during the arrival of sub-mesoscale eddies 1 and 2, when onshore flows were common. These variations were likely due to change in the thermocline depth associated with processes such as internal waves and tidal bores that have been shown to impinge on

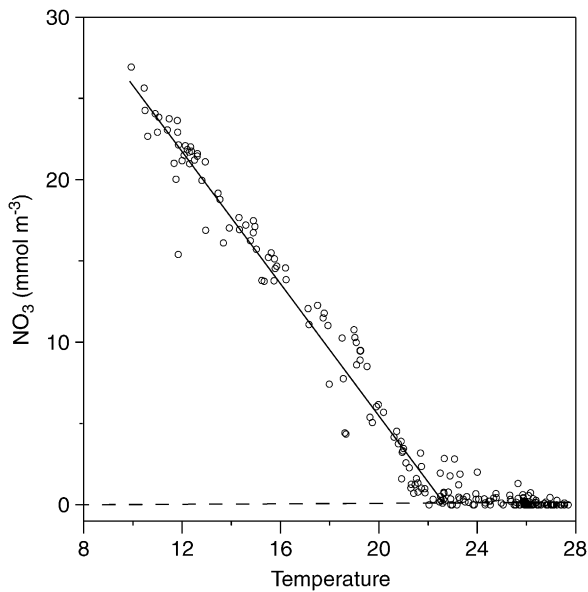


Fig. 12. Nitrate concentrations as a function of temperature from bottle samples taken during Surveys 1 and 2. Note that nitrate was typically undetectable at temperatures greater than 22 °C.

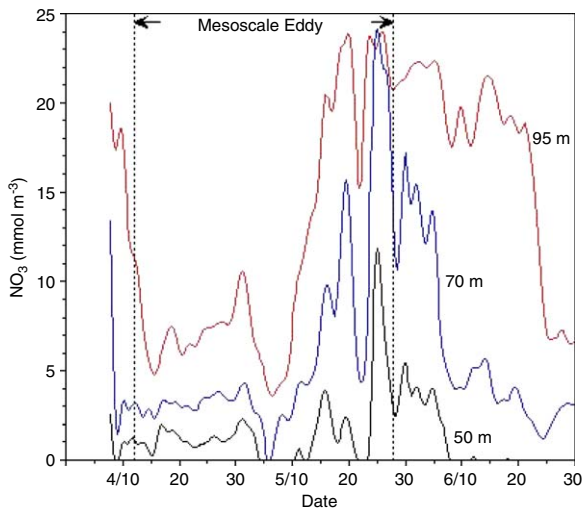


Fig. 13. Subtidal time series of nitrate concentrations extrapolated from the nitrate-temperature relationship of Fig. 12. Temperature was recorded at 50, 70, and 95 m at the ADCP mooring on the 100 m isobath. The passage of the Tortugas Eddy is indicated by the time interval designated as Mesoscale Eddy. Nitrate concentrations appeared to increase following the passage of the eddy center in early May.

Florida reefs during early summer (Leichter et al., 1996, 1998). An increase in high-frequency tidal bore activity with approaching frontal eddies was

also recently reported by Sponaugle et al. (2005) for the outer reefs of the Upper Keys.

Dissolved oxygen, chlorophyll *a* fluorescence, and temperature on the 25 m isobath near LK also responded to the passage of the Tortugas Eddy. The data records are limited to the period of April 25–May 20 due to software problems in the data logger. In vivo fluorescence was relatively low (<120 mV) when the Eddy center was located offshore LK in late April (Fig. 14). This corresponds to the periods of high temperatures and low nitrate concentrations at the 100 m isobath cf. Figs. 11 and 13). Based on the extracted total chlorophyll *a* measurements from CTD stations at mooring 2, the fluorometer values (80–120 mV) correspond to chlorophyll concentrations of ca. 0.05–0.08 mg m<sup>-3</sup>. Following the passage of the Eddy, fluorescence values at mooring 2 increased to 110–160 mV, suggesting a modest increase in chlorophyll biomass. Daily variability was apparent in the fluorescence record with maxima at night, particularly after the passage of the Eddy by May 12 (Fig. 14). Dissolved oxygen also increased and exhibited diel periodicity after the Eddy had passed the mooring (e.g., May 12 and 20). The diel oxygen record attained a maximum at local noon with values of 290 μmol kg<sup>-1</sup>. These oxygen values are near saturation and are interpreted as indicating the diurnal increase is related to phytoplankton gross production and plankton community respiration. At night, in contrast, dissolved oxygen concentrations fell to values of 280–290 μmol kg<sup>-1</sup>. The balance between the diurnal increase and nocturnal decrease in dissolved oxygen suggest there was minimal net community production over 24 h in these oligotrophic waters.

#### 4. Discussion

Mesoscale eddies influence the distribution and productivity of plankton communities through the horizontal mixing and stirring of adjacent waters, and the vertical displacement of the nutricline (Siegel et al., 1999). For example, tilting of isopycnal surfaces and mixing along density surfaces in eddy fronts (Nurser and Zhang, 2000) enhances vertical transport of particulate matter to depth (Tintore et al., 1990), while increased vertical mixing may alter phytoplankton size structure in eddies, and thereby influence the structure of food webs (Rodríguez et al., 2001). The modeling studies of McGillicuddy and Robinson (1997) show that



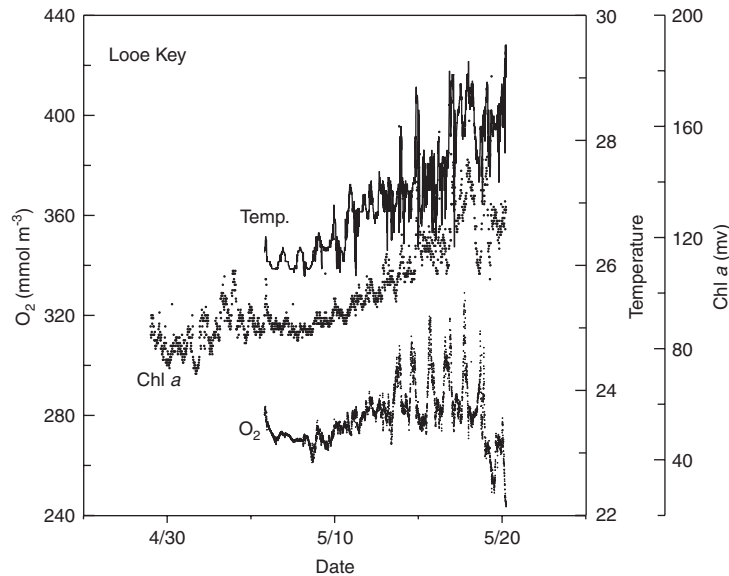


Fig. 14. Time series of temperature, chlorophyll *a* fluorescence (mV), and in situ oxygen concentrations from an instrument package deployed at 7.5 m on the Looe Key mooring (25 m isobath). An insufficient number of chlorophyll samples were taken to accurately calibrate the mooring fluorometer.

eddy pumping forces an uplift of the nutricline into the euphotic zone in cyclonic eddies, potentially elevating rates of new production in the Sargasso Sea on the order of  $0.5 \text{ mol N m}^{-2} \text{ yr}^{-1}$ . These rates of new production are comparable to those derived from oxygen and tracer-based estimates (e.g. Jenkins and Goldman, 1985; Jenkins, 1988). Spatial distributions of sea level anomalies associated with cyclonic eddies in the Sargasso led Siegel et al. (1999) to conclude that nitrate input to the euphotic zone in cyclonic eddies produces an annual nitrogen flux of  $0.24 \text{ mol N m}^{-2} \text{ yr}^{-1}$ , although the magnitude of this potential flux has been recently questioned by Martin and Pondaven (2003). If valid, the rates of nutrient input to the euphotic zone due to eddy pumping would be 10-fold higher than the diapycnal diffusive flux of 'new' nitrogen across the nutricline.

Lee et al. (1992, 1994) hypothesized that pycnocline uplift in Tortugas Eddies could locally enhance plankton productivity in the oligotrophic SSF. Vertical velocities of ca.  $2 \text{ m day}^{-1}$  were derived from potential vorticity estimates in a Tortugas Eddy surveyed near the Dry Tortugas in 1991. The CTD profiles indicated that the thermocline could have shoaled by 25 m at the center of the Eddy, and detectable nitrate was found at 50 m. In the absence of eddies, nitrate concentrations are  $<0.1 \text{ mmol m}^{-3}$  in the upper 50 m of the SSF, and maximum

concentrations are typically  $1\text{--}3 \text{ mmol m}^{-3}$  within the upper 100 m (Lee et al., 1992). We have extrapolated the temperature–nitrate relationship from Fig. 12 to nitrate profiles for CTD 8, 9, 10, and 11. These four CTD stations crossed the Eddy center in Survey 1. The profiles reveal the magnitude of the potential upwelling of nitrate (Fig. 15) and predict that  $>10 \text{ mmol m}^{-3}$  nitrate would be found at 100 m near the Eddy center (CTD 9, 10), as compared to  $7\text{--}8 \text{ mmol m}^{-3}$  at the Eddy perimeter (CTD 8, 11). The depth-integrated nitrate concentration in the upper 100 m at CTD 9 and 10 was nearly 2-fold higher than that at CTD 8 and CTD 11. In the Eddy center the addition of nitrate input to the upper 100 m, relative to the perimeter, would be  $>150 \text{ mmol m}^{-2}$ . Estimated depths of the euphotic zone ( $Z_{\text{eu}}$ ) extrapolated from the light extinction relationship of Smith and Baker (1978) range from 90 to 110 m, with no consistent difference evident in  $Z_{\text{eu}}$  at the Eddy center and perimeter (Fig. 15). However, these estimates of  $Z_{\text{eu}}$  lack a contribution to light extinction by colored dissolved organic matter. Even with this restriction, it is clear that the magnitude of 'new' nitrogen upwelled at Eddy center could potentially enhance primary production.

The extent to which new nutrients enhance productivity in a Tortugas Eddy will reflect the length of time the upwelled waters remain in the

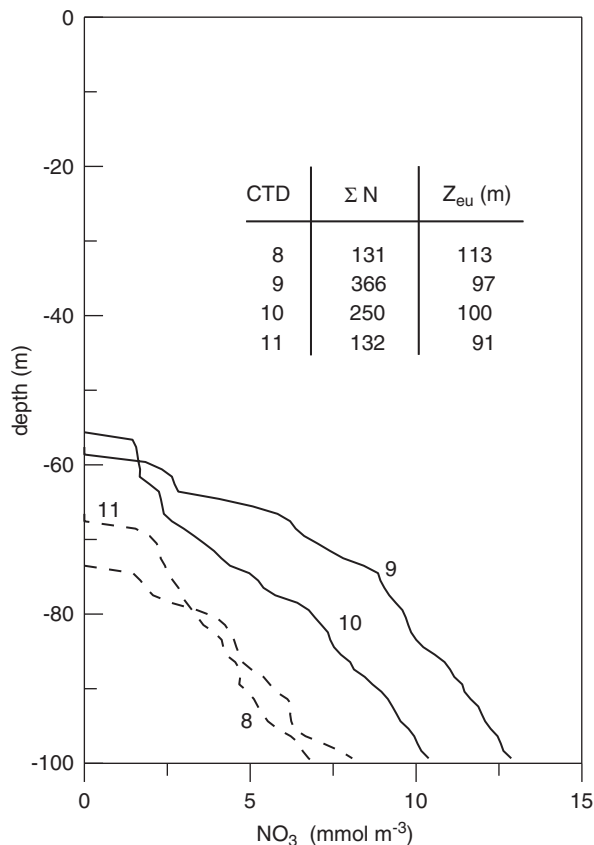


Fig. 15. Vertical profiles of nitrate at CTD stations 8–11 in Transect 3 which crossed the eddy center in Survey 1. Nitrate concentrations are extrapolated from the nitrate-temperature relationship in Fig. 12. The values for the depth-integrated nitrate concentration ( $\Sigma N$ ) are summed from the nitrate profiles at 1 m depth intervals from the surface to 100 m. Concentrations of the depth-integrated  $NO_3$  are as  $mmol NO_3 m^{-2}$ . The estimated depth of the euphotic zone in meters ( $Z_{eu}$ ) corresponds to the 1% isolume depth as derived from Smith and Baker (1978).

euphotic zone, and the time required for the uptake and assimilation of new nutrients by the phytoplankton. Martin and Pondaven (2003) assessed the potential influence of eddy pumping on nutrient utilization in two distinct eddy types. They considered a ‘linear’ eddy in which the feature propagates through the ocean as a wave. In this scenario the nitrate isopleths temporarily shoal into the euphotic zone as the eddy passes any fixed point. Nonlinear eddies, in contrast, are considered Lagrangian features that retain the upwelled high-nitrate waters at the eddy center for the lifetime of the feature. In a nonlinear eddy the nitrate is not replenished by continued upwelling. The two constructs differ in the potential impact of upwelled nutrients on primary

production since nutrients would only be replenished in a linear eddy as it propagates through the sea. The observations from the Tortugas Eddy would suggest that it behaved as a nonlinear feature, since similar nutrient-density relationships were found in Surveys 1 and 2. Since the Tortugas Eddy underwent a rapid elongation in the Middle and Upper Keys during its demise, it might not be surprising that upwelling might have been reduced at the Eddy center. However, rates of nutrient uptake at the base of the euphotic zone are low, typically  $<0.08 mmol N m^{-3} day^{-1}$  (Martin and Pondaven, 2003). This uptake rate would yield a reduction in  $NO_3$  at the base of the euphotic zone over 1 week on the order of  $0.5 mmol N m^{-3}$ . With the scatter in the density-nutrient curves in Survey 2, we could not reliably evaluate the effect of nitrate uptake over 1-week interval between Surveys 1 and 2.

Future studies of cyclonic eddies in oligotrophic waters should constrain the rate of utilization of new nutrients delivered by eddy pumping. The experiment should include measurements of nutrient flux across the pycnocline, new production, and nutrient uptake in eddies during periods of growth and decay. Concurrent tracer releases of  $SF_6$  in the pycnocline could provide direct measures of diffusive fluxes across the upper nutricline that are needed to resolve the debate regarding the magnitude of ‘new’ production attributed to eddy pumping in subtropical gyres.

As in most oligotrophic oceanic waters (e.g., Ortner et al., 1980; Cullen, 1982; Letelier et al., 1996), the SCM was near the nutricline in the Tortugas Eddy (Fig. 9). Previous surveys have reported maximum chlorophyll *a* concentrations of  $0.5 mg m^{-3}$  in the SCM of Tortugas Eddies (Fig. 9c, Lee et al., 1994). However, the prior surveys had limited horizontal and vertical resolution, with three or four CTD stations spaced over distances of 35–40 km, and vertical pigment profiles derived from 4 to 5 sampling depths (Lee et al., 1992, 1994). The improved spatial resolution from our surveys suggests that enhanced phytoplankton biomass, and perhaps enhanced productivity, occurs in the lower euphotic zone in association with a shoaling density interface and nutricline.

Surface chlorophyll *a* concentrations at the center of the Tortugas Eddy, in contrast, were  $<0.10 mg m^{-3}$ ; these values are comparable to mean CZCS-derived pigment levels in the SSF during late spring and early summer (González et al., 2000). Two cloud-free SeaWiFS images in early

May 1999 (<http://seawifs.gsfc.nasa.gov/SEAWIFS.html>) from the LAC archive did not suggest that enhanced surface pigment levels were present near the center of this Tortugas Eddy. The SeaWiFS imagery is consistent with the low surface pigment concentrations measured in the upper euphotic zone. An absence of enhanced surface pigments in the Tortugas Eddy contrasts with surface pigment distributions in cyclonic eddies of the Sargasso Sea where cool surface temperatures are associated with elevated chlorophyll *a* concentrations (McGillicuddy et al., 2001). Shoaling of the pycnocline and nutricline at inertial frequencies has been documented in a Sargasso Sea cyclonic eddy and, combined with eddy pumping, the enhanced nutrient input has been proposed as a mechanism supporting elevated surface pigment levels (McNeil et al., 1999). We lacked the required spatial and temporal resolution to assess any potential role of inertial forcing in the Tortugas Eddy. However our ship-based observations suggest that eddy pumping may have less of a detectable influence on surface pigment levels in Tortugas Eddies than in the cyclonic eddies of the Sargasso Sea. The oligotrophic nature of the surface waters of Tortugas Eddies may be attributed to the vertical separation between the base of the surface mixed layer and the depth of the nutricline. A separation of the mixed layer from the nutricline influences the potential for nutrient limitation in oligotrophic surface waters (Behrenfeld et al., 2002). Mixed layer depths across the width of the 1999 Tortugas Eddy were <15 m; these are similar to a 5 m mixed layer found in a Tortugas Eddy studied in 1991 (Lee et al., 1994). Detectable inorganic nitrogen was found at 55 m, or deeper, in the 1999 Tortugas Eddy (Fig. 15). The vertical separation between the base of surface mixed layer (<15 m) and the nutricline (>55 m) in the Eddy is similar to that observed in the southern North Atlantic subtropical gyre (Behrenfeld et al., 2002). In the subtropical gyre, the bottom of the mixed layer ( $Z_{ml}$ ) is separated from the nutricline by several tens of meters. This vertical separation has been hypothesized as a factor contributing to low net community production in the oligotrophic surface waters of the southern North Atlantic basin (González et al., 2002).

The Tortugas Eddy surveyed in April–May 1999 underwent rapid elongation in the Middle to Upper Keys as the SST surface front of the Florida Current moved toward shore. This convergence compressed the surface signature of the Eddy, and

induced a strong horizontal shear and downstream extension. Onshore convergence of the Eddy-Florida Current surface front may be a typical decay process for Tortugas Eddies. Convergence occurs near the Middle Keys due to a flow adjustment in response to the constraints of the curvature of the Straits of Florida and, the decreasing channel width. The width of the Florida Straits decreases from 170 km off Key West to 85 km off Miami. Thus the Middle Keys are the preferred region of Eddy decay due to topographic constraints. This is analogous to topographic factors near the Charleston Bump and in the South Atlantic Bight (Lee et al., 1991).

The demise of Tortugas Eddies may contribute new nutrients to the outer reefs in the Middle to Upper Florida Keys. As an eddy decays, the eddy center moves towards shore and the pycnocline shoals. The shoaling of cool, high-nutrient isopycnal surfaces occurs seaward of the outer reef, at depths of 50 m or greater. Generally, the nutrient pool remains below the edge of the outer reef, and seaward of the outer reefs at the 30–40 m isobaths. However, on occasion high frequency pulses of cool subsurface waters occur on the outer reefs that elevate nutrient concentrations near the bottom. This was evident in the elevated nitrate concentrations found during Survey 2 near the bottom at the outer reef at MK, AR, and CR (Fig. 7). The bottom temperatures at these CTD stations were all >25°C. The temperature–NO<sub>3</sub> relationship derived from the Tortugas Eddy (Fig. 12) cannot explain the elevated nitrate on the outer reef since it predicts that NO<sub>3</sub> is near undetectable levels at temperatures >22°C. It would appear, therefore, that the subsurface waters of the Tortugas Eddy did not extend onto the outer reef.

However, intrusions of cool, nutrient-rich waters have been observed on the outer reefs of the upper Florida Keys by Leichter, et al. (1996, 1998) and Sponaugle et al. (2005). Their observations have been attributed to internal tidal bores and breaking internal waves on the outer reefs. Sponaugle et al. further found that packets of increased tidal bore activity arrived at the outer reefs with the passage of the leading and trailing wave crests of Tortugas Eddies. These events mainly occur in summer, when seasonal stratification is at an annual maximum. In summer the Florida Current pycnocline impinges further up the slope as part of a seasonal geostrophic adjustment to stronger downstream flow (Brooks and Mooers, 1977; Niiler and Richardson, 1973). Thus the passage and decay of

a mesoscale Tortugas Eddy in the upper Keys could enhance nutrient delivery to the outer reef through upslope intrusions mediated by tidal bores and breaking internal waves.

The cyclonic circulation of Tortugas Eddies may also enhance the delivery of invertebrate and fish larvae to the outer reef. The cyclonic circulation associated with Tortugas Eddies, in combination with onshore flow in response to seasonal wind patterns, has been postulated as a mechanism that retains and concentrates juvenile pink shrimp (*Penaeus duorarum*) near their South Florida nursery grounds (Criales and Lee, 1995). Recruitment of spiny lobster (*Panulirus argus*) and reef fish larvae also likely increases on the Florida Reef Tract when Tortugas Eddies are present (Yeung and Lee, 2002; Porch, 1998; Sponaugle et al., 2002). The westward flow observed at the 100 m isobath during the passage of the Tortugas Eddy at LK (Fig. 10) reinforces the hypothesis that Tortugas Eddies can enhance the delivery of larval fish and invertebrates to the outer reefs. Satellite imagery and the current/temperature time series show that the smaller sub-mesoscale frontal eddies with diameters of ten's of kilometers and lifetimes of several weeks form within the larger, mesoscale Tortugas eddies (Figs. 10 and 11). These smaller vortices form along the Florida Current front in regions of large horizontal shear (e.g., Shay et al., 1998). The opposing alongshore flows at the trailing end of these sub-mesoscale vortices also provides a potential mechanism for concentrating larvae. A strong convergence zone associated with these eddies is characterized by an accumulation of *Sargassum* sp. and marked discontinuities in temperature, salinity and ocean color. Therefore, the sub-mesoscale eddies may concentrate larvae and provide a pulsed delivery to the outer reefs (Sponaugle et al., 2005).

## 5. Conclusions

The passage of a Tortugas Eddy through the SSF results in a shoaling of the pycnocline and nutricline near the Eddy center. In the western SSF the principal effect appears to be enhanced chlorophyll concentrations in the SCM associated with a shoaling of the nutricline. However, the base of the surface mixed layer is separated from the nutricline by >20 m, and this vertical separation may account for a lack of enhanced surface pigment concentrations within these mesoscale cyclonic

eddies. The potential effect of nutrient pumping on the productivity of an Eddy will depend upon the extent to which enhanced nutrients are utilized by phytoplankton near the base of the euphotic zone. Future studies of cyclonic eddies should address this question through simultaneous measurements of plankton productivity and nutrient fluxes, and possibly tracer studies, throughout the lifetime of the feature. The passage of a Tortugas Eddy strongly influences the outer reefs in the Middle and Upper Keys when the Eddy center moves towards shore. A shoaling of the nutricline in decaying Tortugas Eddies could enhance the flux of nutrients to outer reefs of the upper Keys through tidal bores and internal waves. Smaller, sub-mesoscale frontal eddies can be embedded within Tortugas Eddies. Both Tortugas Eddies and the smaller sub-mesoscale eddies likely enhance larval recruitment to the outer reefs.

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## References

- Agustí, S., Duarte, C.M., 1999. Phytoplankton chlorophyll *a* distribution and water column stability in the central Atlantic Ocean. *Oceanologica Acta* 22 (2), 193–203.
- Alexander, J.E., Steele, J.H., Corcoran, E.H., 1961. The seasonal cycle of chlorophyll in the Florida Straits. In: *Proceedings of the Annual Gulf and Caribbean Fisheries Institute*, 14th Annual Session, Miami, pp. 63–67.
- Babu, K.N., Sharma, R., Agarwal, N., Agarwal, V.K., Weller, R.A., 2004. Study of the mixed layer depth variations within the north Indian Ocean using a 1-D model. *Journal of Geophysical Research* 109 (C6), 8016.
- Behrenfeld, M.J., Maranon, E., Siegel, D.A., Hooker, S.B., 2002. Photoacclimation and nutrient-based model of light-saturated photosynthesis for quantifying oceanic primary production. *Marine Ecology Progress Series* 228, 103–117.
- Brooks, D.A., Mooers, C.N.K., 1977. Wind-forced continental shelf waves in the Florida Current. *Journal of Geophysical Research* 82 (18), 2569–2576.

- Causey, B.D., 2002. The role of the Florida Keys National Marine Sanctuary in the South Florida Ecosystem Restoration Initiative. In: Porter, J.W., Porter, K.G. (Eds.), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys*. CRC Press, Boca Raton, FL, pp. 883–894.
- Corcoran, E.F., Alexander, J.E., 1963. Nutrient, chlorophyll, and primary production studies in the Florida Current. *Bulletin of Marine Science* 13, 527–541.
- Criales, M.M., Lee, T.N., 1995. Larval distribution and transport of penaeoid shrimps during the presence of the Tortugas Gyre in May–June 1991. *Fishery Bulletin* 93 (3), 471–482.
- Cullen, J.J., 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Canadian Journal of Fisheries and Aquatic Sciences* 39 (5), 791–803.
- Davis, R.F., Moore, C.C., Zaneveld, J.R.V., Napp, J.M., 1997. Reducing the effects of fouling on chlorophyll estimates derived from long-term deployments of optical instruments. *Journal of Geophysical Research* 102 (C3), 5851–5855.
- Falkowski, P.G., Ziemann, D., Kolber, Z., Bienfang, P.K., 1991. Role of eddy pumping in enhancing primary production. *Nature* 352 (6330), 55–58.
- Fratantoni, P.S., Lee, T.N., Podesta, G.P., Muller-Karger, F., 1998. The influence of Loop Current perturbations on the formation and evolution of Tortugas eddies in the southern Straits of Florida. *Journal of Geophysical Research* 103 (C11), 24,759–24,779.
- González, N., Anadón, R., Maraño, E., 2002. Large-scale variability of planktonic net community metabolism in the Atlantic Ocean: importance of temporal changes in the oligotrophic subtropical waters. *Marine Ecology Progress Series* 233, 21–30.
- González, N.M., Müller-Karger, F.E., Estrada, S.C., de los Reyes, R.P., del Río, I.V., Pérez, P.C., Arenal, I.M., 2000. Near-surface phytoplankton distribution in the western Intra-Americas Sea: the influence of El Niño and weather events. *Journal of Geophysical Research* 105 (C6), 14029–14043.
- Gordon, L.I., Jennings Jr., J.C., Ross, A.A., Krest, J.M., 1993. A suggested protocol for continuous flow automated analysis of seawater nutrients (phosphate, nitrate nitrite and silicic acid) in the WOCE Hydrographic Program and the joint Global Ocean Flux Study, In: *WOCE Operations Manual*, 3.1.3, WHP Operations and Methods Manual, 91-1.
- Hitchcock, G.L., Mariano, A.J., Rossby, T., 1993. Mesoscale pigment fields in the Gulf Stream: observations in a meander crest and trough. *Journal of Geophysical Research* 98 (C5), 8425–8445.
- Holm-Hansen, O., Riemann, B., 1978. Chlorophyll *a* determination: improvements in methodology. *Oikos* 30, 438–447.
- Jenkins, W.J., 1988. Nitrate flux into the euphotic zone near Bermuda. *Nature* 331 (6156), 521–523.
- Jenkins, W.J., Goldman, J.C., 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. *Journal of Marine Research* 43 (2), 465–491.
- Keller, B.D., Itkin, A., 2002. Shoreline nutrients and chlorophyll *a* in the Florida Keys, 1994–1997: a preliminary analysis. In: Porter, J.W., Porter, K.G. (Eds.), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys*. CRC Press, Boca Raton, FL, pp. 649–658.
- Lee, T.N., Mayer, D.A., 1977. Low frequency variability and spin off eddies along the shelf off southeast Florida. *Journal of Marine Research* 35 (1), 193–220.
- Lee, T.N., Williams, E., 1999. Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *Bulletin of Marine Science* 64 (1), 35–56.
- Lee, T.N., Yoder, J.A., Atkinson, L.P., 1991. Gulf Stream frontal eddy influence on productivity of the Southeast US Continental Shelf. *Journal of Geophysical Research* 96 (C12), 22,191–22,205.
- Lee, T.N., Rooth, C., Williams, E., McGowan, M., Szmant, A.F., Clarke, M.E., 1992. Influence of Florida Current, gyres and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. *Continental Shelf Research* 12 (7–8), 971–1002.
- Lee, T.N., Clark, M.E., Williams, E., Szmant, A.F., Berger, T., 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bulletin of Marine Science* 54 (3), 621–646.
- Lee, T.N., Leaman, K., Williams, E., Berger, T., Atkinson, L., 1995. Florida Current meanders and gyre formation in the southern Straits of Florida. *Journal of Geophysical Research* 100 (C5), 8607–8620.
- Leichter, J.J., Wing, S.R., Miller, S.L., Denny, M.W., 1996. Pulsed delivery of subthermocline water to Conch reef (Florida Keys) by internal tidal bores. *Limnology and Oceanography* 41 (7), 1490–1501.
- Leichter, J.J., Shellenbarger, G., Genovese, S.J., Wing, S.R., 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? *Marine Ecology Progress Series* 166, 83–97.
- Letelier, R.M., Dore, J.E., Winn, C.D., Karl, D.M., 1996. Seasonal and interannual variations in photosynthetic carbon assimilation at Station ALOHA. *Deep-Sea Research II* 43 (2–3), 467–490.
- Limouzy-Paris, C.B., Graber, H.C., Jones, D.L., Röpke, A.W., Richards, W.J., 1997. Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. *Bulletin of Marine Science* 60 (3), 966–983.
- Martin, A.P., Pondaven, P., 2003. On estimates of the vertical nitrate flux due to eddy pumping. *Journal of Geophysical Research* 108 (C11), 3359.
- McGillicuddy Jr., D.J., Robinson, A.R., 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea. *Deep-Sea Research Part I* 44 (8), 1427–1450.
- McGillicuddy Jr., D.J., Johnson, R., Siegel, D.A., Michaels, A.F., Bates, N.R., Knap, A.H., 1999. Mesoscale variations of biogeochemical properties in the Sargasso Sea. *Journal of Geophysical Research* 104 (C6), 13,381–13,394.
- McGillicuddy Jr., D.L., Kosnyrev, V.K., Ryan, J.P., Yoder, J.A., 2001. Covariation of mesoscale ocean color and sea-surface temperature patterns in the Sargasso Sea. *Deep-Sea Research II* 48 (8–9), 1823–1836.
- McNeil, J.D., Jannasch, H.W., Dickey, T., McGillicuddy Jr., D.L., Brzezinski, M., Sakamoto, C.M., 1999. New chemical, bio-optical and physical observations of upper ocean response to the passage of a mesoscale eddy off Bermuda. *Journal of Geophysical Research* 104 (C7), 15,537–15,548.
- Niiler, P.P., Richardson, W.S., 1973. Seasonal variability of the Florida Current. *Journal of Marine Research* 31 (3), 144–167.
- Nurser, A.J.G., Zhang, J.W., 2000. Eddy-induced mixed layer shallowing and mixed layer/thermocline exchange. *Journal of Geophysical Research* 105 (C9), 21,851–21,868.



- Ortner, P.B., Wiebe, P.H., Cox, J.L., 1980. Relationships between oceanic epizooplankton distributions and the seasonal deep chlorophyll maximum in the northwestern Atlantic Ocean. *Journal of Marine Research* 38 (3), 507–531.
- Porch, C.E., 1998. A numerical study of larval fish retention along the southeast Florida coast. *Ecological Modelling* 109 (1), 35–59.
- Rodríguez, J., Tintoré, J., Allen, J.T., Blanco, J.M., Gomis, D., Reul, A., Ruiz, J., Rodríguez, V., Echevarría, F., Jiménez-Gómez, F., 2001. Mesoscale vertical motion and the size structure of phytoplankton in the ocean. *Nature* 410 (6826), 360–363.
- Shay, N., Lee, T.N., Williams, E.J., Graber, H.C., Rooth, C., 1998. Effects of low-frequency current variability on near-inertial sub-mesoscale vortices. *Journal of Geophysical Research* 103, 18,691–18,714.
- Siegel, D.A., McGillicuddy, D.J., Fields, E.A., 1999. Mesoscale eddies, satellite altimetry, and new production in the Sargasso Sea. *Journal of Geophysical Research* 104 (C6), 13,359–13,379.
- Smith, R.C., Baker, K.S., 1978. The bio-optical state of ocean waters and remotes sensing. *Limnology and Oceanography* 23 (2), 247–259.
- Sponaugle, S., Cowen, R.K., Shanks, A., Morgan, S.G., Leis, J.M., Pineda, J., Boehlert, G.W., Kingsford, M.J., Lindeman, K.C., Grimes, C., Munro, J.L., 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bulletin of Marine Science* 70 (1), 341–375.
- Sponaugle, S., Lee, T., Kourafalou, V., Pinkard, D., 2005. Florida Current frontal eddies and the settlement of coral reef fishes. *Limnology and Oceanography* 50 (4), 1033–1048.
- Szmant, A.M., Forrester, A., 1996. Water column and sediment nitrogen and phosphorus distribution patterns in Florida Keys, USA. *Coral Reefs* 15 (1), 21–41.
- Tintore, J., Wang, D.-P., La, Violette, P.E., 1990. Eddies and thermohaline intrusions of the shelf/slope front off the northeast Spanish coast. *Journal of Geophysical Research* 95 (C2), 1627–1633.
- Vargo, G.A., 1968. Studies of phytoplankton ecology in tropical and subtropical environments of the Atlantic Ocean. Part 2. Quantitative studies of phytoplankton distribution in the Straits of Florida and its relation to physical factors. *Bulletin of Marine Science* 18 (1), 5–60.
- Yeung, C., Lee, T.N., 2002. Larval transport and retention of the spiny lobster, *Panulirus argus*, in the coastal zone of the Florida Keys, USA. *Fisheries Oceanography* 11 (5), 286–309.